Mem. Qd Mus. **20**(1): 65–75 pls. 1–3 [1980].

PROCOELOUS CROCODILE FROM LOWER CRETACEOUS OF LIGHTNING RIDGE, N.S.W.

R.E. MOLNAR
Queensland Museum

ABSTRACT

Restudy of the type material and study of referred material of the Lower Cretaceous *Crocodylus (Bottosaurus) selaslophensis* indicates that the material is referable to neither *Crocodylus* nor *Bottosaurus*. Referred material includes procoelous cervical centra and suggests that the crocodile is an eusuchian. Distinguishing characters are a dentary with alveolar groove and medical shelf, procoelous cervicals, caudal transverse processes excavated posteriorly at their bases, and caudal neurocentral suture extending onto the transverse process. All known material derives from a small area of the Griman Creek Fm. at Lightning Ridge, New South Wales.

Crocodilian fossils are common in the Quaternary and late Tertiary of Australia (e.g. De Vis 1885; Longman 1924, 1925; Molnar 1976; Archer and Wade 1978; Gorter and Nicoll 1978). Miocene crocodilians, still largely under study, are also common at some localities. Earlier crocodilians have only rarely been reported in Australia. Riek (1952) reported crocodilian skin impressions (QUF 10625) from the probably Eocene Redbank Plains Series. These impressions show roughly hexagonal scales with distinct growth lines and lacking keels, a combination of features not known to occur in crocodilians. The general pattern of the scales could not be matched with that of any living crocodilian from the Australasian region, and thus it is unlikely that these skin impressions derive from a crocodilian. Riek (1952) also reported an angular from the Redbank Plains Series, thus demonstrating that crocodilians were present.

Etheridge (1917) described the earliest known Australian crocodile as *Crocodylus (Bottosaurus) selaslophensis*, from the Cretaceous opal-bearing beds at Lightning Ridge, New South Wales. While other crocodilian material from this site had already been obtained by the Australian Museum, Etheridge described only the type jaw fragment. Since 1917 further material has been discovered there, including procoelous cervical vertebrae. This material, like almost all found at the Ridge, was not in association, so it is possible that more than one taxon is involved. The duplicated left tibiae demonstrate that at least two individuals are represented. However all known material derives from individuals of approximately the same size, and among the latest discoveries I have seen teeth matching those in the type jaw indicating that elements possibly deriving from the same individual are still being found. In the absence of any indication that more than one taxon is represented, I shall assume that all pieces derive from a single species.

All fossil bones known from Lightning Ridge are opalized, at least in part, and thus many of the specimens have been retained by their discoverers and are represented in museum collections by plaster or resin casts.

Although Etheridge assigned the jaw fragment to *Crocodylus (Bottosaurus)* there is no indication in the literature that anyone else ever considered *Bottosaurus* a subgenus or a synonym of *Crocodylus*. Indeed *Bottosaurus* is usually classified (e.g. Steel 1973) as an alligatorine rather than a crocodyline.

COLLECTION DESIGNATIONS: AM — Australian Museum; QM — Queensland Museum; QUF — University of Queensland, Dept. of Geology.

Geology of Lightning Ridge

Nowhere at Lightning Ridge are there any extensive exposures of the opal-bearing beds. The geology of these beds has thus been interpreted entirely from features observed in the opal mines and the single large open cut and from the fossils collected from these mines. Earlier work on the stratigraphy of the Ridge (e.g. Whiting and Relph 1961) has been superseded by that of Byrnes (1977). He has concluded that the opal-bearing beds at the Ridge form the southern portion of the Griman Creek Formation which is more extensively exposed in southern Queensland. In New South Wales this formation is subdivided into two members, the Wallangulla Sandstone and the Coocoran Claystone. The opals (and fossils) occur in the Finch clay facies of the Wallangulla Sandstone Member.

Byrnes (1977) concludes that the Wallangulla Sandstone was deposited in estuarine conditions. In addition to fossil bone, pelecypods and gastropods have been found. None of the pelecypods represent clearly marine taxa (Byrnes 1977), while some of the gastropods are members of the family Viviparidae, which are fresh water forms. The occurrence of the fossil bones is such as to suggest transport: only in one instance were any found in articulation. Most of the elements seen are such as can be easily transported, e.g. femora, phalanges, teeth, centra, with no flat bones or ribs. The largest elements identifiable were plesiosaurian. Some of the bones appear to have been worn or broken prior to fossilisation, and one plesiosaur element had been bored. Plant material, including conifer cones, is reasonably common. Byrnes (1977) reports that some cross-bedding is present, and what appear to be impressions of plant roots occur in the clay facies. All of this suggests an estuarine environment of deposition.

Description

Mandible: Etheridge figured and described a fragment of crocodilian dentary with six teeth in situ (AM F15818) as the type of *Crocodylus selaslophensis* (Plate 1, E and G). The teeth are thecodont (as in all other known crocodilians) and not pleurodont as Etheridge stated: the bony partitions separating sequential alveoli are distinct. These partitions terminate below the level of the dorsal margin of the dentary so that the teeth are set in an alveolar groove. Slight anterior and posterior carinae are present on the crowns and striae are absent.

A medial shelf extends along the tooth row, giving the dentary the appearance of being wider than in *Crocodylus*. The lateral surface of the dentary is sculptured with longitudinal ridges and grooves much as modern *Crocodylus*. A prominent mass of opal along the medial surface (Plate 1, E) represents either a displaced bone fragment or an opalised mass of matrix, and not a projection from the dentary. There is no indication that this piece is from the symphyseal region as reported by Etheridge.

Maxilla: A small fragment (AM F18628) probably represents the anterior extremity of the right maxilla, with one tooth in place (Plate 1, F and H). Two other alveoli are present, one empty, the other occupied by only the root. The single crown is conical, medially flexed, and has fine striae but no carinae. The fragment as a whole is dorsoventrally compressed, suggesting a low, broad snout, and is lightly sculptured.

Cervicals: Two cervical vertebrae have been seen, the more complete represented by a cast (QM F9507), and the other a centrum in the Anderson collection that is also represented by a cast (QM F10240). Both centra are clearly procoelous, the anterior faces deeply concave, and the posterior convexities rimmed by a flange as in modern crocodilians. The posterior convexity of the Anderson centrum (Plate 2) is incomplete, and the anterior central face is worn, but appears to be slightly inclined upwards. This centrum is 18·5 mm long as preserved.

Both centra are constricted at the middle with marked ventral keels that descend anteriorly to form small, blunt hypophyses. Bases of both parapophyses and diapophyses are present on QM F9507 (Fig. 1), but absent from Anderson's specimen. The centrum of QM F9507 is 16·4 mm long, 15 mm high at the anterior face and 13 mm wide across that face. In general form and proportions both centra resemble cervical centra of the living species of *Crocodylus*.

Two portions of a cervical neural arch (AM F60081), although not sharing a contact, may derive from the same vertebra (Plate 2, D). Neurocentral articular facets, the base of the neural spine, the diapophyses, the left prezygapophysis and the base of the right are preserved. The arch is from a mid-cervical about 30 per cent larger than QM F9057. The neural spine is set anterior to the postzygapophyses, and both pre- and postzygapophyseal facets were more nearly horizontal than in *Crocodylus americanus* (Mook

1921, fig. 3). The arch resembles those of *Crocodylus porosus* in these features. The diapophyses are placed well above the neurocentral suture, as in the second cervical of *C. porosus*.

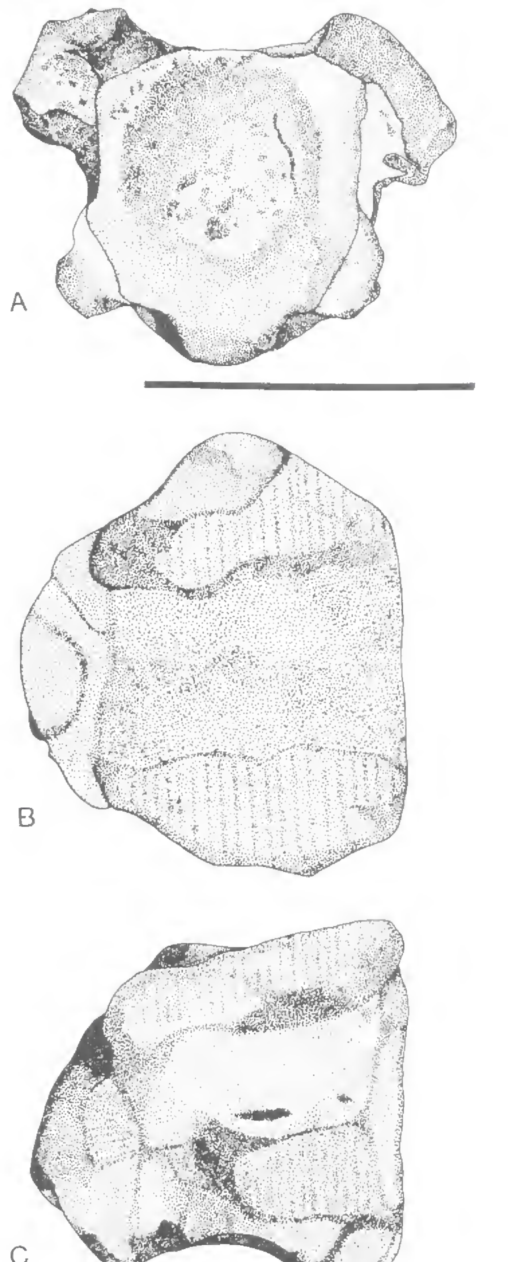


FIG. 1: Crocodilian cervical centrum from Lightning Ridge. (Specimen lost, represented by cast QM F8507.) Bar represents 2 cm. A, anterior view; B, dorsal view; C, lateral view.

SACRAL: The single sacral centrum (AM F15819) includes the lower portion of the neural arch with prezygapophyses, the entire left sacral rib and the base of the right (Plate 3). In general form this element greatly resembles the first sacrals of *'Leidyosuchus' multidentatus* (Mook 1930, fig. 5) and of *Diplocynodon hantoniensis* (Owen 1884, there given as *Crocodilus hastingsiae*). The prezygapophyseal facets are more nearly horizontal in this sacral than in the first sacral of either of these taxa, being inclined at only 25° to the horizontal. The anterior face of the centrum is shallowly concave, broad (23 mm wide by 12 mm high), and slightly inclined downwards. The posterior face is incomplete, less broad, almost flat (with but a shallow central concavity) and is slightly inclined dorsally. The centrum is 24 mm long, as is the sacral rib which bears a posteriorly inclined iliac articular surface. A distinct ridge extends from the prezygapophysis laterally along the anterodorsal edge of the rib. The ventral surface of the centrum is faintly concave with slight longitudinal ridges along both sides.

CAUDAL: The proximal caudal centrum (AM F60080) includes portions of both diapophyses and the right prezygapophysis (Pl. 2), and is 28 mm long, 13 mm high and 12 mm wide at the anterior face. The central articular faces are inclined as in the single known sacral. The centrum is constricted at the middle, with two sharp ventral keels much like those of the caudals of *Holopsisuchus brevispinus* (Cope 1869, Pl. IV, fig. 4). Both central faces are concave as preserved, but both are worn so it is not certain that the centrum was amphicoelous. The neurocentral suture was dorsal to the diapophyses and zygapophyses and extended laterally 12 mm onto the dorsal surface of the transverse process. A distinct pocket extends into the posterior margin of the transverse process just lateral to the postzygapophysis.

CERVICAL RIB: The proximal portion of a cervical rib (AM F60082), from the left side, does not differ from those of *Crocodylus porosus*.

FEMUR: An incomplete element possibly representing the distal one-third of a right femur is present in the collection of K. Barlow (Plate 1, A and B). The specimen is badly worn, but has less curvature in the shaft than femora of *Crocodylus*.

TIBIA: Two left tibiae are preserved, the distal end missing from both. The smaller (AM F18630) is less than 10 per cent smaller than the larger (AM F15821) (Plate 1, C and D). In both the cnemial crest is badly worn. These two tibiae are identical and closely resemble those of *C. porosus*, from which they differ only in that the lateral surface of the shaft is flat with a sharper anterolateral border and a less marked posterolateral border.

DISCUSSION

Etheridge's type specimen (AM F15818), a dentary, is characterised by: 1) an alveolar groove and 2) a medial shelf. Assuming that the other crocodilian material is referable to the same taxon, it is further characterised by: 3) a low, probably broad snout; 4) procoelous cervicals, with a small hypophysis; 5) keeled caudal centra; 6) excavated caudal diapophyses; and 7) caudal neurocentral suture extended onto diapophysis. Postcranial elements resemble those of crocodylids in the forms of the cervical and sacral vertebrae, and of the tibia. This general resemblance, together with the procoelous character of the cervical centra, suggests that this crocodilian was eusuchian.

The type jaw fragment of *Crocodylus selaslophensis* was compared by Etheridge with a jaw fragment referred to *Bottosaurus harlani* (most recently figured by Mook, 1925, fig. 8). The latter specimen is attributed to an immature individual. There is no clear evidence of immaturity of the Lightning Ridge crocodile, although the caudal neural arch has separated from the centrum at the neurocentral suture, as has the cervical neural arch (but not that of the sacral). Mature teeth of *B. harlani* are considerably more bulbous and blunt than in the Lightning Ridge form, and neither the type jaw of *B. harlani* nor the referred immature specimen exhibit an alveolar groove. Thus the Lightning Ridge crocodilian is not referable to *Bottosaurus*.

The alveolar groove and the excavated caudal transverse processes suggest that this form is also not referable to *Crocodylus*. The genus *Crocodylus* is not otherwise known to range into the Lower Cretaceous (cf. Steel 1973), and the three reported Lower Cretaceous English species (*C. cantabrigiensis*, *C. icenicus*, and *C. saulii*) have not been reviewed since the nineteenth century and are of uncertain significance. *C. saulii* may be congeneric with *Bernissartia fagesii* (Buffetaut, 1975).

Other than *'Crocodylus' selaslophensis*, only two crocodilians exhibit an alveolar groove: *Edentosuchus tienshanensis* (Young, 1973) and *Macelognathus vagans* (March 1884, Ostrom 1971). Both are currently referred to the Mesosuchia, and both differ from the Lightning Ridge crocodile (and from each other) in several other characters; no close relationship is warranted.

Procoelous vertebrae, considered characteristic of eusuchians, also occur in a mesosuchian (Joffe 1967), and reportedly in a sebecosuchian (Arid and Vizotto 1965). The mesosuchian is *Theriosuchus*, an atoposaurid. Atoposaurids have been suggested as possible ancestors of eusuchians (Joffe 1967; see also Langston 1973). However the known atoposaurids are all considerably smaller than the individuals represented at Lightning Ridge and all date from the Upper Jurassic. None are reported in the literature to exhibit excavated caudal diapophyses, an alveolar groove, or several of the other characters of the Lightning Ridge crocodile. In the absence of further evidence it may be assumed that the Lightning Ridge crocodilian is not a large atoposaurid.

The sebecosuchian *Baurusuchus* also reportedly had procoelous vertebrae (Arid and Vizotto 1965). The type jaw and maxillary fragment from the Ridge show none of the dental specializations of sebecosuchians, so that reference to this group can also be ruled out. Unfortunately the vertebrae of *Baurusuchus* were not illustrated so that comparison of the vertebrae cannot presently be made.

The occurrence of a procoelous crocodilian in the Lower Cretaceous (Aptian or Albian) of Australia is unexpected. *Hylaeochampsa vectiana*, usually recognised as the earliest known eusuchian (Romer 1966, Steel 1973), comes from the Lower Cretaceous of England. The Lower Cretaceous *Bernissartia fagesii*, often considered eusuchian (e.g. Charig 1967) has recently been demonstrated to be a mesosuchian (Buffetaut, 1975). *Heterosuchus valdensis*, also from the Lower Cretaceous of western Europe, is often considered congeneric with *Hylaeochampsa* (Romer 1966, Steel 1973). While *Hylaeochampsa* is known only from cranial material, *Heterosuchus* is known from postcranial material, including procoelous vertebrae. The three Lower Cretaceous species attributed to *Crocodylus*, as mentioned previously, need restudy. The described vertebrae of *C. cantabrigiensis* and *C. icenicus* are procoelous, and generally resemble those from Lightning

Ridge (Seeley 1874, 1976). All these forms are from western Europe.

The earliest extra-European eusuchians (*Aegyptosuchus*, *Stomatosuchus*, and *Stromerosuchus*) appear in North Africa around the Cenomanian, although a procoelous vertebra has been found in the Albian of Algeria (Buffetaut pers. comm., 1979) and by the latest Cretaceous eusuchians were widespread and diverse. Thus the indication of a possible eusuchian in the Aptian or Albian of New South Wales suggests a considerably wider range of procoelous crocodilians during the Lower Cretaceous than has been generally recognised.

The holotype of Etheridge's *Crocodylus* (*Bottosaurus*) *selaslophensis* is too incomplete for confident comparison with other specimens. However it is sufficiently unique (see the character states listed on p. 136) that should more complete material be found, the taxon would be both recognisable and diagnosible. Further, the Griman Creek Formation has been so little explored for fossils that it is premature to relegate Etheridge's species to the status of *nomen vanum* until it is clear that more complete topotype material is not forthcoming.

SUMMARY

Procoelous cervical vertebrae from the Griman Creek Fm. (probably Albian) of Lightning Ridge, New South Wales, demonstrate the existence of a procoelous crocodilian in Australia during the Lower Cretaceous. Assuming that all the remains pertain to a single taxon, that taxon is characterised by procoelous cervicals, excavated caudal transverse processes and caudal neurocentral suture extending onto the transverse processes. This material probably pertains to *Crocodylus selaslophensis* Etheridge (1917). The type dentary fragment of that species has an alveolar groove and a medial shelf establishing that there is no reason to refer this species to the genus *Crocodylus*. The species is regarded as indeterminate pending the discovery of further material from the Griman Creek Fm.

ACKNOWLEDGMENTS

Dr Alex Ritchie provided access to the specimens in the Australian Museum, and Dr Mary Wade drew my attention to the material in her care at the Queensland Museum. Their encouragement at the beginning of this study is greatly appreciated. Dr D. Baird, of Princeton University, kindly provided information on adult *Bottosaurus*. Mr G. Anderson and Mr K. Barlow kindly loaned specimens from their respective private collections for study, Mr R. Jones of the Australian Museum and Miss K. Brown of the School of Zoology, University of New South Wales, also provided material assistance for this study. The photographic illustrations were prepared with the assistance of the Department of Biomedical Illustration, Prince of Wales Hospital, and the photographic department of the Queensland Museum; the drawings are by Ms L. Crevola-Gillespie.

LITERATURE CITED

ARCHER, M. and WADE, M., 1976. Results of the Ray E. Lemley expeditions, part 1. The Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland. *Mem. Qd Mus.* **17**: 379–97.

ARID, F.M., and VIZOTTO, L.D., 1965. Crocodilideos fosseis nas proximidades de Santa Adelia (SP). *Cienc. Cultura* **17**: 138–9.

BUFFETAUT, E., 1975. Sur l'anatomie et la position systematique de *Bernissartia fagesii* Dollo, L., 1883, crocodilien du Wealdien de Bernissart, Belgique. *Bull. Inst. r. Sci. nat. Belg., Sci. Terre.* **51**: 1–20.

BYRNES, J.G., 1977. Notes on the Rolling Downs Group in the Milparinka, White Cliffs and Angledool 1:250,000 sheet areas. *Geol. Surv. New South Wales, Rept.* GS1977/005: 1–17.

CHARIG, A.J., 1967. Reptilia. *In* APPLEBY, R.M., et al. 'The Fossil Record, a Symposium with Documentation'. 827 pp. (Geological Society of London: London).

COPE, E.D., 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Trans. Amer. Phil. Soc.* **14**: 34–61.

DE VIS, C.W., 1885. On remains of an extinct saurian. *Proc. Roy. Soc. Qd* **2**: 181–91.

ETHERIDGE, R., JR., 1917. Reptilian notes: *Megalania prisca*, Owen, and *Notiosaurus dentatus*, Owen; lacertilian dermal armour; opalized remains from Lightning Ridge. *Proc. Roy. Soc. Vic.* (ns) **29**: 127–33.

GORTER, J.D., and NICOLL, R.S., 1978. Reptilian fossils from Windjana Gorge, Western Australia. *J. Roy. Soc. W. Australia* **60**: 97–104.

JOFFE, J., 1967. The 'dwarf' crocodiles of the Purbeck Formation, Dorset; a reappraisal. *Palaeontology* **10**: 629–39.

LANGSTON, W., JR., 1973. The crocodilian skull in historical perspective. In, Gans, C., and Parsons, T.S., eds. 'Biology of the Reptilia', vol. 4 Morphology D. 539 pp. (Academic Press: London).

LONGMAN, H.A., 1924. Some Queensland fossil vertebrates. *Mem. Qd Mus.* **8**: 16–28.

1925. A crocodilian fossil from Lansdowne Station. *Mem. Qd Mus.* **8**: 103–8.

MARSH, O.C., 1884. A new order of extinct Jurassic reptiles (Macelognatha). *Amer. J. Sci.* (3) **27**: 341.

MOLNAR, R.E., 1976. Crocodile with laterally compressed snout: first find in Australia. *Science* **197**: 62–4.

MOOK, C.C., 1921. Notes on the postcranial skeleton in the Crocodilia. *Bull. Amer. Mus. Nat. Hist.* **44**: 67–100.

1925. A revision of the Mesozoic Crocodilia of North America. *Bull. Amer. Mus. Nat. Hist.* **51**: 319–432.

1930. A new species of crocodilian from the Torrejon beds. *Amer. Mus. Nov.* **447**: 1–11.

OSTROM, J.H., 1971. On the systematic position of *Macelognathus vagans*. *Postilla* **153**: 1–10.

OWEN, R., 1884. 'A History of British Fossil Reptiles.' 856 pp. (Cassell & Co.: London).

RIEK, E.F., 1952. The fossil insects of the Tertiary Redbank Plains Series. Part I: an outline of the fossil assemblage with descriptions of the fossil insects of the orders Mecoptera and Neuroptera. *Univ. Qd Papers, Dept. Geol.* **4**: 3–14.

ROMER, A.S., 1966. 'Vertebrate Paleontology', third edition. 468 pp. (Univ. of Chicago Press: Chicago).

SEELEY, H.G., 1874. On cervical and dorsal vertebrae of *Crocodilus cantabrigiensis* (Seeley) from the Cambridge Upper Greensand. *Quart. J. Geol. Soc. London* **30**: 693–5.

1876. On *Crocodilus icenicus* (Seeley), a second and larger species of crocodile from the Cambridge Upper Greensand, contained in the Woodwardian Museum of the University of Cambridge. *Quart. J. Geol. Soc. London* **32**: 437–9.

SKWARKO, S.K., 1973. A correlation chart for the Cretaceous system in Australia. *Bur. Miner. Resources, Bull.* **126**: 55–63.

STEEL, R., 1973. Crocodylia. In, Kuhn, O., ed. 'Encyclopedia of Paleoherpetology', vol. 16. 116 pp. (Gustav Fischer Verlag: Stuttgart).

YOUNG C., 1973. A new fossil crocodile from Wuerho. *Mem. Inst. Vert. Paleo. Paleoanthro., Acad. Sin.* **11**: 37–44. (In Chinese).

WHITING, J.W., and RELPH, R.E., 1961. The occurrence of opal at Lightning Ridge and Grawin, with geological notes on County Finch. *Tech. Rept., N.S.W. Dept. Mines* **6**: 7–21.

PLATE 1

A: Distal end of ?femur from Lightning Ridge (Barlow collection) posterior aspect.

B: The same, medial aspect. Bar represents 1 cm.

C: Crocodilian tibia from Lightning Ridge (AM F15821) medial aspect.

D: The same, anterior aspect. Bar represents 2 cm.

E: The mandibular fragment (holotype) of *Crocodylus (Bottosaurus) selaslophensis* (AM F15818), dorsal aspect.

F: Crocodilian maxillary fragment from Lightning Ridge (AM F18628), lateral aspect.

G: The mandibular fragment, lateral aspect. Bar represents 1 cm. Unbroken surface is present around the specimen beneath the third and fourth teeth, thus the full depth of the mandible is represented at that point.

H: The maxillary fragment, ventral aspect. Bar represents 1 cm.

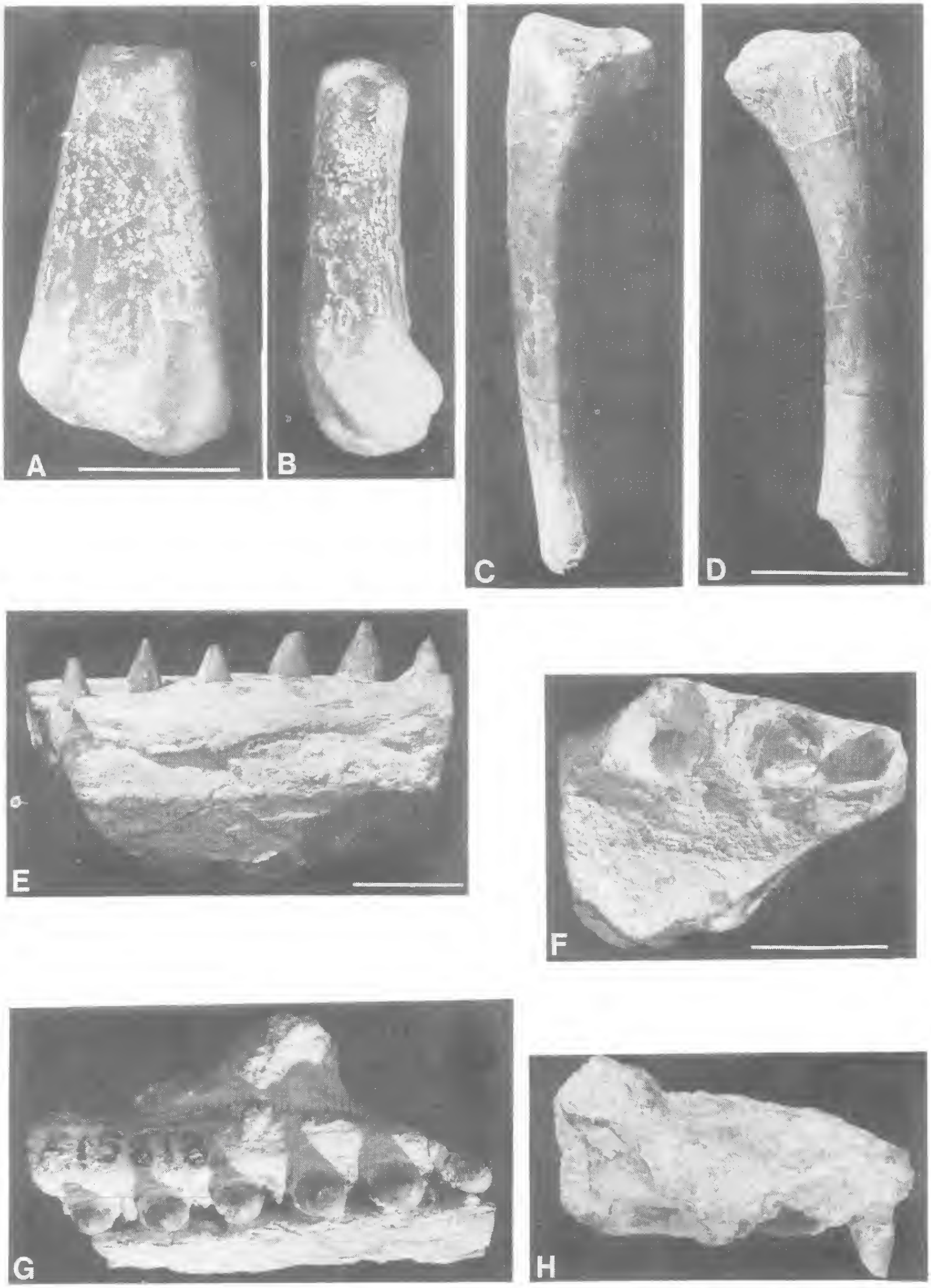

A
B
C
D
E
F
G
H

PLATE 2

A and B: Crocodilian cervical centrum from Lightning Ridge, A, dorsal and B, lateral aspect of centrum in the Anderson collection. Bar represents 2 cm.

C: Crocodilian caudal vertebra from Lightning Ridge (AM F60080) lateral aspect. Bar represents 2 cm.

D: Incomplete cervical neural arch of crocodilian from Lightning Ridge, anterior aspect (AM F60081). Diagonal hatching indicates glue connecting the two portions. Bar represents 2 cm.

E: The caudal vertebra (AM F60080), ventral aspect.

F: The same, dorsal aspect.

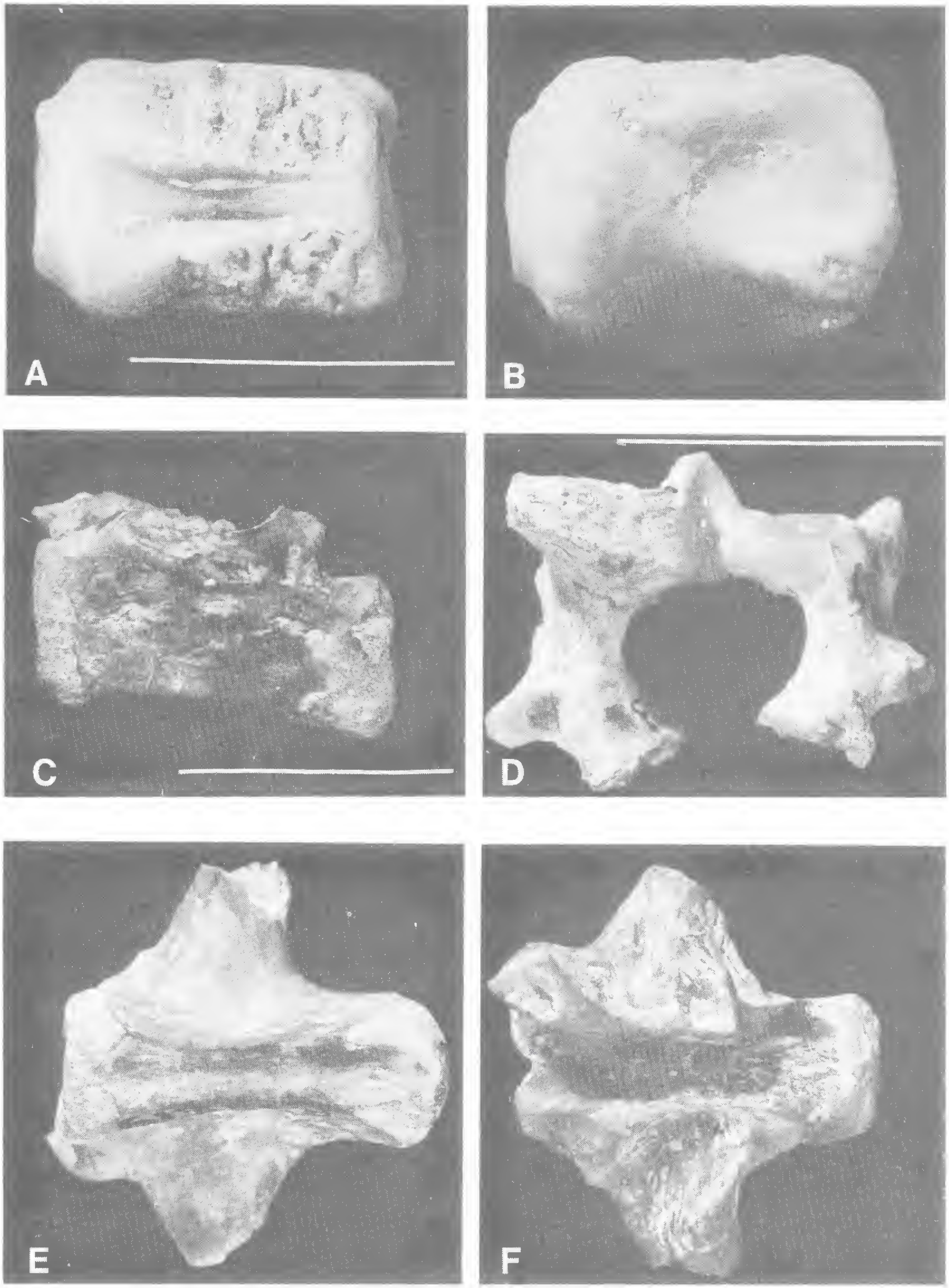
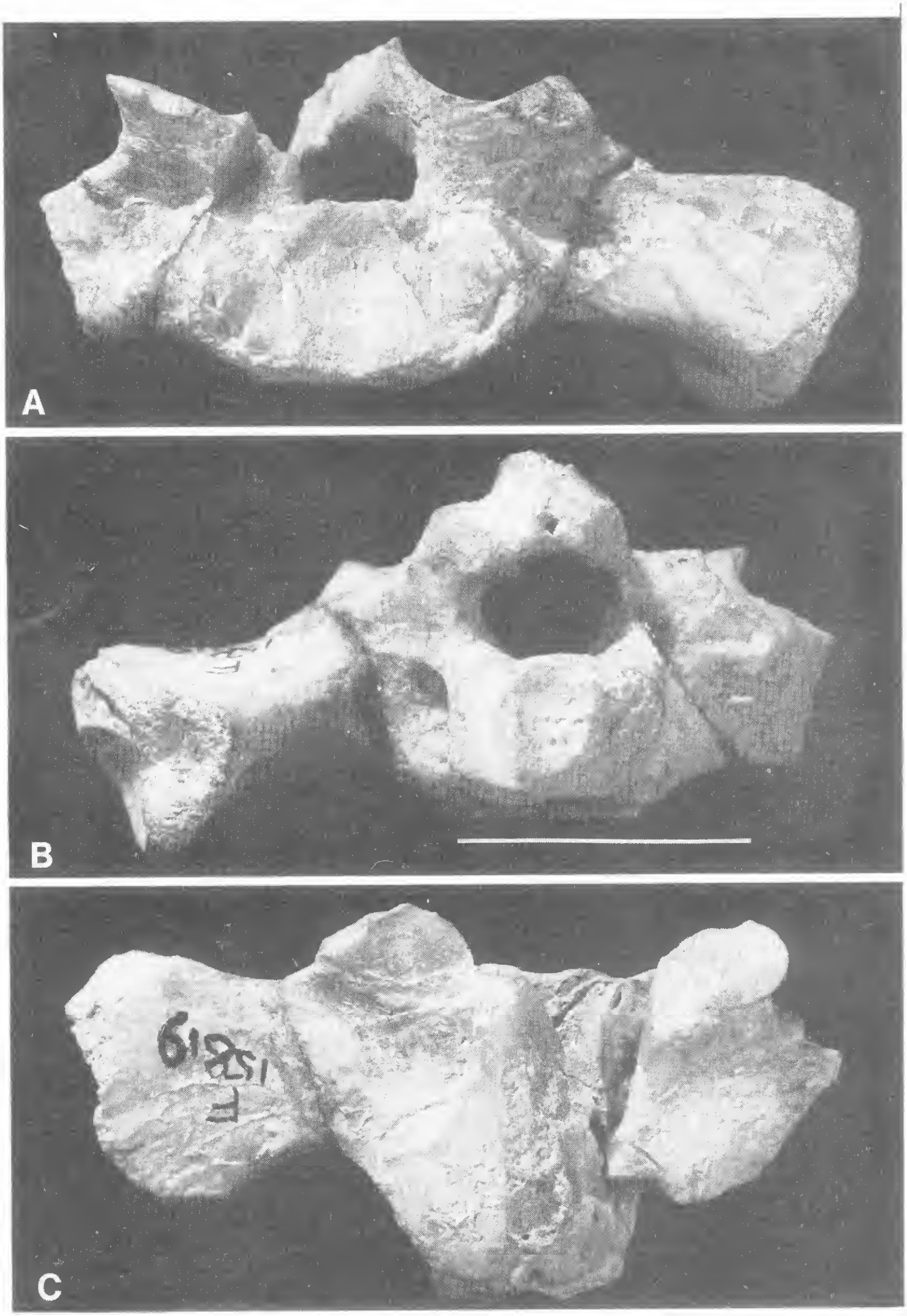

A
B
C
D
E
F

PLATE 3

A: Crocodilian sacral vertebra from Lightning Ridge (AM F15719) ventral aspect.

B: The same, posterior aspect.


A
B
C